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conducted. The measurements of pressure were made by the simplest possible means, and it was only by great experimental skill and care that even approximate results could be obtained.

Such criticisms, however, do not mar the magnificent success of Hall's experiments. For nearly a hundred years, in spite of the advance of physical and chemical science, no substantial improvement on his results was attained. His work was immediately recognized as trustworthy and conclusive, and became a classic in the literature of experimental geology. Although not exactly the founder of this school of research, for Spallanzani and De Saussure had made fusion experiments on rocks before his time, he placed the subject in a prominent position among the departments of geological investigation, and did great service in supporting Hutton's theories by evidence of a new and unexpected character.

SOME PROBLEMS IN EVOLUTION

By Professor EDWIN S. GOODRICH, F.R.S.

PRESIDENT OF THE ZOOLOGICAL SECTION

IN all probability factors of inheritance exist, and the fundamental problem of biology is how are the factors of an organism changed, or how does it acquire new factors? In spite of its vast importance, it must be confessed that little advance has been made towards the solution of this problem since the time of Darwin, who considered that variation must ultimately be due to the action of the environment. This conclusion is inevitable, since any closed system will reach a state of equilibrium and continue unchanged, unless affected from without. To say that mutations are due to the mixture or reshuffling of pre-existing factors is merely to push the problem a step farther back, for we must still account for their origin and diversity. The same objection applies to the suggestion that the complex of factors alters by the loss of certain of them. To account for the progressive change in the course of evolution of the factors of inheritance and for the building up of the complex it must be supposed that from time to time new factors have been added; it must further be supposed that new substances have entered into the cycle of metabolism, and have been permanently incorporated as self-propagating ingredients entering into lasting relation with pre-existing factors. We are well aware that living protoplasm contains molecules of large size and extraordinary complexity, and that it may be urged that by their combination in different ways, or by the mere regrouping of the atoms within them, an almost infinite number of changes may result, more than sufficient to account for the mutations which appear. But this does not account for the building up of the original complex. If it must

be admitted that such a building process once occurred, what right have we to suppose that it ceased at a certain period? We are driven, then, to the conclusion that in the course of evolution new material has been swept from the banks into the stream of germ-plasm.

If one may be allowed to speculate still further, may it not be supposed that factors differ in their stability?—that whereas the more stable are merely bent, so to speak, in this or that direction by the environment, and are capable of returning to their original condition, as a gyroscope may return to its former position when pressure is removed, other less stable factors may be permanently distorted, may have their metabolism permanently altered, may take up new substance from the vortex, without at the same time upsetting the system of delicate adjustments whereby the organism keeps alive? In some such way we imagine factorial changes to be brought about and mutations to result.

Let it not be thought for a moment that this admission that factors are alterable opens the door to a Lamarckian interpretation of evolution! According to the Lamarckian doctrine, at all events in its modern form, a character would be inherited after the removal of the stimulus which called it forth in the parent. Now of course, a response once made, a character once formed, may persist for longer or shorter time according as it is stable or not; but that it should continue to be produced when the conditions necessary for its production are no longer present is unthinkable. It may, however, be said that this is to misrepresent the doctrine, and that what is really meant is that the response may so react on and alter the factor as to render it capable of producing the new character under the old conditions. But is this interpretation any more credible than the first?

Let us return to the possible alteration of factors by the environment. Unfortunately there is little evidence as yet on this point. In the course of breeding experiments the occurrence of mutations has repeatedly been observed, but what led to their appearance seems never to have been so clearly established as to satisfy exacting critics. Quite lately, however, Professor M. F. Guyer, of Wisconsin, has brought forward a most interesting case of the apparent alteration at will of a factor or set of factors under definite well-controlled conditions.⁷ You will remember that if a tissue substance, blood-serum for instance, of one animal be injected into the circulation of another, this second individual will tend to react by producing an anti-body in its blood to antagonise or neutralise the effect of the foreign serum. Now Professor Guyer's ingenious experiments and results may be briefly summarised as follows. By repeatedly injecting a fowl with the substance of the lens of the eye of a rabbit he obtained anti-lens serum. On injecting this 'sensitised' serum into a pregnant female rabbit it

⁷*American Naturalist*, vol. lv. 1921; *Jour. of Exper. Zoology*, vol. xxxi. 1920.

was found that, while the mother's eyes remained apparently unaffected, some of her offspring developed defective lenses. The defects varied from a slight abnormality to almost complete disappearance. No defects appeared in untreated controls, no defects appeared with non-sensitised sera. On breeding the defective offspring for many generations these defects were found to be inherited, even to tend to increase and to appear more often. When a defective rabbit is crossed with a normal one the defect seems to behave as a Mendelian recessive character, the first generation having normal eyes and the defect reappearing in the second. Further, Professor Guyer claims to have shown that the defect may be inherited through the male as well as the female parent, and is not due to the direct transmission of anti-lens from mother to embryo *in utero*.

If these remarkable results are verified, it is clear that an environmental stimulus, the anti-lens substance, will have been proved to affect not only the development of the lens in the embryo, but also the corresponding factors in the germ-cells of that embryo; and that it causes, by originating some destructive process, a lasting transmissible effect giving rise to a heritable mutation.

Professor Guyer, however, goes farther, and argues that, since a rabbit can also produce anti-lens when injected with lens substance, and since individual animals can even produce anti-bodies when treated with their own tissues, therefore the products of the tissues of an individual may permanently affect the factors carried by its own germ-cells. Moreover he asks, pointing to the well-known stimulative action of internal secretions (hormones and the like), if destructive bodies can be produced, why not constructive bodies also? And so he would have us adopt a sort of modern version of Darwin's theory of Pangenesis, and a Lamarckian view of evolutionary change.

But surely there is a wide difference between such a poisonous or destructive action as he describes and any constructive process. The latter must entail, as I tried to show above, the drawing of new substances into the metabolic vortex. Internal secretions are themselves but characters, products (perhaps of the nature of ferments behaving as environmental conditions, not as self-propagating factors, moulding the responses, but not permanently altering the fundamental structure and composition of the factors of inheritance.

Moreover, the early fossil vertebrates had, in fact, lenses neither larger nor smaller on the average than those of the present day. If destructive anti-lens had been continually produced and had acted, its effect would have been cumulative. A constructive substance must, then, have also been continually produced to counteract it. Such a theory might perhaps be defended; but would it bring us any nearer to the solution of the problem?

The real weakness of the theory is that it does not escape from the fundamental objections we have already put forward as fatal to

Lamarckism. If an effect has been produced, either the supposed constructive substance was present from the first, as an ordinary internal environmental condition necessary for the normal development of the character, or it must have been introduced from without by the application of a new stimulus. The same objection does not apply to the destructive effect. No one doubts that if a factor could be destroyed by a hot needle or picked out with fine forceps the effects of the operation would persist throughout subsequent generations.

Nevertheless, these results are of the greatest interest and importance, and, if corroborated, will mark an epoch in the study of heredity, being apparently the first successful attempt to deal experimentally with a particular factor or set of factors in the germ-plasm.

There remains another question we must try to answer before we close, namely, 'What share has the mind taken in evolution?' From the point of view of the biologist, describing and generalising on what he can observe, evolution may be represented as a series of metabolic changes in living matter moulded by the environment. It will naturally be objected that such a description of life and its manifestations as a physico-chemical mechanism takes no account of mind. Surely, it will be said, mind must have affected the course of evolution, and may indeed be considered as the most important factor in the process. Now, without in the least wishing to deny the importance of the mind, I would maintain that there is no justification for the belief that it has acted or could act as something guiding or interfering with the course of metabolism. This is not the place to enter into a philosophical discussion on the ultimate nature of our experience and its contents, nor would I be competent to do so; nevertheless, a scientific explanation of evolution cannot ignore the problem of mind if it is to satisfy the average man.

Let me put the matter as briefly as possible at the risk of seeming somewhat dogmatic. It will be admitted that all the manifestations of living organisms depend, as mentioned above, on series of physico-chemical changes continuing without break, each step determining that which follows; also that the so-called general laws of physics and of chemistry hold good in living processes. Since, so far as living processes are known and understood, they can be fully explained in accordance with these laws, there is no need and no justification for calling in the help of any special vital force or other directive influence to account for them. Such crude vitalistic theories are now discredited, but tend to return in a more subtle form as the doctrine of the interaction of body and mind, of the influence of the mind on the activities of the body. But, try as we may, we cannot conceive how a physical process can be interrupted or supplemented by non-physical agencies. Rather do we believe that to the continuous physico-chemical series of events there corresponds a continuous series of mental events inevitably connected with it; that the two series are but partial views

or abstractions, two aspects of some more complete whole, the one seen from without, the other from within, the one observed, the other felt. One is capable of being described in scientific language as a consistent series of events in an outside world, the other is ascertained by introspection, and is describable as a series of mental events in psychical terms. There is no possibility of the one affecting or controlling the other, since they are not independent of each other. Indissolubly connected, any change in the one is necessarily accompanied by a corresponding change in the other. The mind is not a product of metabolism as materialism would imply, still less an epiphenomenon or meaningless by-product as some have held. I am well aware that the view just put forward is rejected by many philosophers, nevertheless it seems to me to be the best and indeed the only working hypothesis the biologist can use in the present state of knowledge. The student of biology, however, is not concerned with the building up of systems of philosophy, though he should realise that the mental series of events lies outside the sphere of natural science.

The question, then, which is the more important in evolution, the mental or the physical series, has no meaning, since one cannot happen without the other. The two have evolved together *pari passu*. We know of no mind apart from body, and have no right to assume that metabolic processes can occur without corresponding mental processes, however simple they may be.

Simple response to stimulus is the basis of all behaviour. Responses may be linked together in chains, each acting as a stimulus to start the next; they can be modified by other simultaneous responses, or by the effects left behind by previous responses, and so may be built up into the most complicated behaviour. But owing to our very incomplete knowledge of the physico-chemical events concerned, we constantly, when describing the behaviour of living organisms, pass, so to speak, from the physical to the mental series, filling up the gaps in our knowledge of the one from the other. We thus complete our description of behaviour in terms of mental processes we know only in ourselves (such as feeling, emotion, will) but infer from external evidence to take place in other animals.

In describing a simple reflex action, for instance, the physico-chemical chain of events may appear to be so completely known that the corresponding mental events are usually not mentioned at all, their existence may even be denied. On the contrary, when describing complex behaviour when impulses from external or internal stimuli modify each other before the final result is translated into action, it is the intervening physico-chemical processes which are unknown and perhaps ignored, and the action is said to be voluntary or prompted by emotion or the will.

The point I wish to make, however, is that the actions and behaviour of organisms are responses, are characters in the sense de-

scribed in the earlier part of this address. They are inherited, they vary, they are selected, and evolve like other characters. The distinction so often drawn by psychologists between instinctive behaviour said to be inherited and intelligent behaviour said to be acquired is as misleading and as little justified in this case as in that of structural characters. Time will not allow me to develop this point of view, but I will only mention that instinctive behaviour is carried out by a mechanism developed under the influence of stimuli, chiefly internal, which are constantly present in the normal environmental conditions, while intelligent behaviour depends on responses called forth by stimuli which may or may not be present. Hence, the former is, but the latter may or may not be inherited. As in other cases, the distinction lies in the factors and conditions which produce the results. Instinctive and intelligent behaviour are usually, perhaps always, combined, and one is not more primitive or lower than the other.

It would be a mistake to think that these problems concerning factors and environment, heredity and evolution, are merely matters of academic interest. Knowledge is power, and in the long run it is always the most abstruse researches that yield the most practical results. Already, in the effort to keep up and increase our supply of food, in the constant fight against disease, in education, and in the progress of civilisation generally, we are beginning to appreciate the value of knowledge pursued for its own sake. Could we acquire the power to control and alter at will the factors of inheritance in domesticated animals and plants, and even in man himself, such vast results might be achieved that the past triumphs of the science would fade into insignificance.

Zoology is not merely a descriptive and observational science, it is also an experimental science. For its proper study and the practical training of students and teachers alike, well-equipped modern laboratories are necessary. Moreover, if there is to be a useful and progressive school contributing to the advance of the science, ample means must be given for research in all its branches. Life doubtless arose in the sea, and in the attempt to solve most of the great problems of biology the greatest advances have generally been made by the study of the lower marine organisms. It would be a thousand pities, therefore, if Edinburgh did not avail itself of its fortunate position to offer to the student opportunities for the practical study of marine zoology.

In his autobiography, Darwin complains of the lack of facilities for practical work—the same need is felt at the present time. He would doubtless have been gratified to see the provision made since his day and the excellent use to which it has been put; but what seems adequate to one generation becomes insufficient for the next. We earnestly hope that any appeal that may be made for funds to improve this department of zoology may meet with the generous response it certainly deserves.